ANALYSIS OF STACKED SPECIES DISTRIBUTION MODELS PROVIDES A NEW PERSPECTIVE ON BIOGEOGRAPHY AND CONSERVATION OF PHILIPPINE AMPHIBIANS

BY

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Submitted to the graduate degree program in Ecology & Evolutionary Biology and the Graduate Faculty of the University of Kansas in partial fulfillment of the requirements for the degree of Master of Arts.

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Date Defended: July 13th, 2016

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ABSTRACT

In regions of the megadiverse tropics where biodiversity information is scarce, species distribution models have become important tools for conservation. Use of models, generated individually, for many species or an entire fauna enables researchers to quantify measures of diversity through the use of a Presence-Absence Matrix (PAM). In this study we calculated two biodiversity indices (species richness and average locality range size) for 96 native Philippines amphibian species based on all globally available occurrence data from biodiversity repositories. We then investigated Philippine amphibian biodiversity patterns and examined how these patterns change in relation to the geological components of the archipelago (island groups), its many volcanic elevational gradients, and finally to the Philippine government protected areas. The results of our study suggest that the species richness peaks at intermediate elevation, a result consistent with recent field transect studies. The Mindanao and Luzon Pleistocene Aggregate Island Complexes have the highest species richness and are inhabited by species that on average have markedly large geographical ranges. The central portion of the geologically distinct Palawan Island (and, to a lesser extent, Mindoro Island) has high to intermediate species richness but is inhabited by species that have much smaller average geographical ranges. We are encouraged by a general congruence between Philippine protected areas and biodiversity areas of highest amphibian diversity, but we also note several geographical pockets of high amphibian diversity that currently are unprotected, as well as protected area coverage of low-diversity sites. This analysis, the first of its kind for any terrestrial vertebrate group in the Philippines, demonstrates the practical utility of PAM analysis of stacked distribution models, and Range-Diversity ordination for biogeographical studies, ecological applications, and conservation planning.

ACKNOWLEDGEMENTS- We thank KU Ecological Niche Modeling group, KU herpetology lab and KU informatics for their assistant throughout this project.

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INTRODUCTION

The spatially explicit study of biodiversity patterns has a range of both applied (Villalobos & Arita 2010; Villalobos et al. 2013) and more theoretical (Arita et al. 2008; 2011; Soberon & Ceballos 2011) implications for conservation of biological diversity. Seeking to identify and understand fundamental, reoccurring, and/or predictable patterns of species distributions, biogeographers have, in turn, posited hypotheses relating the distribution of biodiversity to geographical barriers, climatic variation, and ecological gradients (Wallace 1877, MacArthur 1972, Brown 1995). The interaction of species' ecology (biotic and abiotic environment, species interactions) and evolutionary history (range evolution, colonization history, evolutionary niche conservatism/lability) clearly influences the geographical patterns of biological diversity we observe today (Wines & Donoghue 2003; Graham et al. 2014, Peterson 2001).

In this study, we investigated geographical patterns of species diversity in native Philippine amphibian species. Because of its geological history (with structured, well defined biogeographical regions centered on island groups with a known history of Pleistocene connectivity) and its numerous volcanic elevational gradients (that have led to repeated stratification of species into forest types and climate zones) this archipelago represents an excellent natural laboratory to test hypotheses concerning the origin, accumulation, and partitioning, of terrestrial vertebrate species (Dickerson 1928; Brown & Alcala 1970; Brown & Siler 2013; Brown et al. 2013, 2016). The current configuration of the archipelago (composed of both paleo-transported, accreted, landmasses, and former Pleistocene Aggregate Island Complexes [PAICs] that are now subdivided by shallow marine channels), its complex and highly variable climate, and its extreme altitudinal topographical heterogeneity (Adams and Pratt 1911; Feliciano and Pelaez 1940; Rutland 1968; Hashimoto 1981a, 1981b; Auffenberg 1988;

Hall 1996; 1998) have all been implicated in studies that have sought to determine how and when terrestrial biodiversity arrived at, or originated in this unique archipelago (Inger 1854; Diamond & Gilpin 1983; Heaney 1986; Jansa et al. 2006; Esselstyn and Brown 2009; Esselstyn et al. 2009, 2011; Oliveros and Moyle 2010; Siler et al. 2012; Oaks et al. 2013).

Approximately 118 described and 56 undescribed species are native to the archipelago (Brown et al. 2013; Diesmos et al. 2015); in this project, we modeled their geographical distributions and studied patterns of overlap in and range size for 96 native Philippine amphibian species (taxa for which sufficient occurrence data exist in biodiversity repository databases available in the public domain).

We focused our efforts on accumulating occurrence data, generating biogeography- and phylogeny-informed (constrained to the geographical space accessible to the species) species distribution models (Peterson AT et al. 2011) and calculating two-biodiversity indices (species richness and average locality range size—the average size of the geographical ranges of all the species at a given site) which we visualized in a spatially explicit Presence/Absence Matrix (PAM) analysis. We interpret observed patterns in the context of geological history, climate patterns, and topological relief in the archipelago. In this paper we summarize the current knowledge of patterns of distribution in native Philippine amphibian fauna and ask how diversity and geographical range size are related to each other across archipelago. Our use of Range-Diversity plots allow us identify unique amphibian-specific characteristics of the archipelago's geography that have immediate conservation implications. Finally, we then examined congruence between the amphibian biodiversity the Philippine government protected area network; this exercise identifies several areas of diversity–protection mismatch, and deficiency that should become the focus of protected area establishment in the immediate future.

MATERIALS AND METHODS

We developed species distribution models for each species (a total of 96 models) using Maxent (Phillips et al. 2006) via an extension to Quantum GIS (http://www2.qgis.org/en/site/), as follows. The occurrence data for this project were obtained from GBIF (http://www.gbif.org), the University of Kansas Herpetology database (http://collections.biodiversity.ku.edu/KUHerps/), and previously unpublished records from field notes, collections in Natural History of the Philippines and observations assembled by RMB and colleagues. We also used Google Earth to assign geographic coordinates to records from known localities that were not accompanied by coordinates in the original record, and verified and quality-controlled the points for each species by plotting them on geography and checking for consistency. We converted the csv files to shapefiles and reprojected the point shapefiles that were in WGS 1984 datum format to Asia South Equal Area Conic (EPSG: 102028).

We used a set of 5 layers (2.5' resolution) of climate data (max temperature of warmest month, min temperature of coldest month, annual precipitation, precipitation of wettest month and precipitation of driest month) that were clipped to island boundaries. A first set of shapefiles was created based on Pleistocene Aggregate Island Complex (PAIC) boundaries (Brown et al. 2013), and developed sets of masks limited to hypothesized accessible areas (Barve et al. 2011) that were customized for each species based on (1) PAIC boundaries, (2) distributions of sister-species relationships from numerous phylogenetic studies (see Broen et al. 2013 for review), and (3) known biogeographic barriers and zones of concentrated turnover of species' distributions.

We posted the point shapefiles and climate data to LifeMapper and assembled the climate datasets using the Lifemapper plugin in QGIS (Cavner, Jeffery A. 2015). We then attributed shapefiles as holding presence, absence, and no data, and rasterized them to the exact resolution and extent of the climate data using GDAL. Points and corresponding masks were uploaded and the algorithm parameterized using the client library (https://github.com/qgis/QGIS-Web-Client). Next, we linked the points with the masks and posted the experiments to the grid-based computing facility with point ids, mask ids, scenario ids and algorithm parameters. The Maxent output grids (median values, ASCII formats) were reprojected and converted to GeoTiff format in QGIS. We enabled custom plugin dialog using the points for each layer to build adjusted least training presence thresholds (Peterson 2014) and convert the raw outputs to binary models.

Finally, based on the 'library' of binary maps for each species, we converted the maps to a presence-absence matrix (PAM) using the Lifemapper plugin (Cavner 2015). We calculated species richness and average range size of species at each site across the country also using the Lifemapper plugin (Cavner 2015). These values were then linked to shapefiles and projected on to the archipelago's geography. We explored the spatial relationships of PAICs (each of 7 major island groups that are now recognized as fauna regions), elevational relief (positions of major montane areas) to geographical concentrations of amphibian species diversity. We also examined the correspondence (or lack thereof) between amphibian biodiversity and Philippine national protected areas. Specifically, we ask (1) which Philippine faunal zones, situated on the various geological platforms of islands separated by shallow seas (PAICs), are home to the highest and lowest levels of endemic amphibian species diversity? (2) Which of the PAICs are home to species with the largest and smallest ranges? (3) Are land-bridge islands like Palawan more or less diverse than oceanic islands? (4) How do areas of high amphibian species diversity spatially related to the major mountain ranges and volcanic peaks within the larger islands of the archipelago? (5) And finally, does the current Philippine government protected area network adequately include or coincide with the areas of highest amphibian diversity?

RESULTS

We created "M-constrained" (biogeographically- and phylogeny-informed) species distribution models for 96 native Philippine amphibian species with sufficient occurrence data (≥ 5 points). We excluded 30 species because they either have extremely small geographic distributions and/or are currently represented by too few unique occurrences. Future studies will include all species, once a more suitable method (under development; JS *unpublished* data) to model these species with extremely small ranges. Species richness and the average range size were calculated for each 2.5' (5 km^2) pixel across the Philippines from the stacks of 96 individual binary (thresholded) species distribution models.

Mapping these our biodiversity indices on geography of the archipelago allowed initial visualization of basic patterns. Qualitative assessment of emergent patterns readily provides resolution of several of research objectives. First, it is clear that the Mindanao PAIC, the largest island group situated at the southern extent of the archipelago (FIGURE 1) is home to the highest concentrations of species diversity observed here. The largest island within the PAIC (Mindanao, itself) has multiple pockets of extremely high diversity, as do the islands that were connected to Mindanao at multiple times frames during the Pleistocene (Bohol, Leyte and Samar islands; review: Brown and Diesmos 2009). Smaller islands of the West Visayan PAIC (particularly the notoriously deforested Cebu Island; Brown & Alcala 1986; Supsup et al. in press), Mindoro Island, and islands of the Romblon PAIC (Romblon, Tablas, and Sibuyan; Siler et al. 2012) emerged as the least amphibian-diverse areas in our study. Finally, perhaps surprisingly, although the Luzon and Palawan PAICs are large and topographically complex, these faunal regions possessed mixed patterns: areas of extremely low diversity (such as the Cagayan River Valley of north Luzon, the west coast, Pampanga Plains, and Zambales Mountains; Brown et al. 1996; Devan-Song and Brown 2012), combined with pockets of moderate to high amphibian diversity. The latter included the northern Cordillera Mountain Range [Diesmos et al. 2004; Brown et al. 2012], the entirety of the east coast Sierra Madre Mountain Range [Brown et al. 2013], and in particular, the area of their intersection (the Caraballo Mountains and central east coast Aurora Province area) where herpetological faunal studies have previously noted high levels of species diversity (Brown et al. 2000; Siler et al. 2011).

Qualitatively, there are correspondence between montane areas, and regions of particularly high species diversity (FIGURES 1A, 1B). Relating species richness to elevations showed that species richness is highest at higher elevation. We investigated this relationship by plotting the species richness values against the elevation. Via this manipulation, we could discern that high species richness (25–30 species at a given site) is concentrated in central Palawan, in the Cordillera Mountain Range of northern Luzon, in the Sierra Madre Mountain Range of northern Luzon, and the highlands of Mindanao and several islands of the Mindanao |PAIC (Bohol, Leyte, Samar, and Basilan) and that highest species richness occurs at intermediate elevations. More moderate, or intermediate levels of species richness (10–15 species) is found in islands of the Western Visayas PAIC (e.g., southern Negros, Panay) Mindoro Island, several islands of the Luzon PAIC (Marinduque, Polillo, Masbate islands) and the Bicol Peninsula of southeastern Luzon. The rest of islands are associated with low species richness (FIGURE 1A).

As expected some of the smallest ranges (1583-33009 km^2) observed were concentrated on small islands, like Tawi Tawi, Jolo, Calayan, Batanes Islands, the Babuyan Islands, and many other small islands. However, exceedingly small species ranges also occurred on large islands like Palawan and also in northeastern and central Luzon (i.e., the Cagayan River Valley lowlands between the Sierra Madre and Cordillera ranges). The next-smallest average local range sizes (33099- 64436 km^2) were on Negros, Cebu, Panay, Masbate, Mindoro, and Polillo, all islands with some degree of isolation, and the Sierra Madre and Cordillera ranges. In contrast, the species with the largest geographical ranges observed in this study the residents of the Mindanao PAIC (Samar, Leyte, Bohol, and parts of Mindanao Island; FIGURE 1C).

We observed correspondence between high species richness and large average locality range size: throughout the archipelago, regions with higher species richness coincidenced geographically with taxa having larger average range. We also note cases of non-correspondence or difference between the two biodiversity indices: particularly in central Palawan which exhibits intermediate species richness but composed of species with small average locality range size. Similarly, the islands of Mindoro, Western Visayas (e.g., Negros, and Masbate) Marindeque Island and coastal regions all exhibit low species richness, but contain taxa with intermediate sized geographical ranges. A unique mismatch was observed on Cebu Island, which shows low species richness of taxa with large average geographical ranges. Finally, Bohol was found to possess high species richness in the higher elevation areas of the southern parts of the island but the remaining portions of island have low diversity, composed of taxa occupying wide geographic distributions (FIGURES 1A, 1C).

Our range-diversity projections (RD) proved useful for exploring the relationship between species richness and the average locality range size. This allowed for the identification of emergent properties: biogeographically anomalous regions, geographical areas, or entire islands characterized by unique combinations of varying levels of species richness and average locality range size. The regions with highest species richness and largest average locality range sizes fall in the Mindanao PAIC: Mindanao Island itself, southern Bohol, Samar, Leyte and Basilan. The regions with low to intermediate species richness and also low average locality range sizes are in central Palawan, parts of central Luzon, northern Romblon Island, and the Pampanga Plains of Luzon. The areas with the lowest species richness but composed of taxa with the largest geographical ranges the amphibians of northern Palawan, the northwest coast of Luzon, part of the Bicol Peninsula of Luzon, and Metro Manila, including Batagas and Cavite (FIGURE 2).

Our results demonstrate that areas of high levels of amphibian biodiversity coincide reasonably well with Philippine protected areas; however, a few regions have high species richness (and average locality range size) and occur outside of protected areas. These include cases unique and in some cases reasonably well forested areas such as the entire central highlands of Leyte Island, the majority of the mountainous Zamboanga Peninsula, southern portions of the Cordillera Mountain Range of Luzon (e.g., north of

Sagada), the expansive southeast "Cotobato Coast" of Mindanao, and mountains along the northern coast of Mindanao. Finally, we note instances of protected regions that do not coincide with high species richness or the average locality range size. The most obvious areas that fall into this category are northern Palawan and the Batanes Islands (FIGURE 3).

DISCUSSION

Our analysis results in the first geographically explicit, quantitative characterization of Philippine amphibian megadiversity, generated from stacked distribution models and a presence-absence matric (PAM) analysis. To the best of our knowledge, ours is the first study to quantitatively describe the archipelago's spatial amphibian biodiversity patterns (but see Taylor 1928; Inger 1954) and make use of the Philippine amphibian occurrence records (see Diesmos et al. 2015 for occurrence dot maps of all the species, generated from ≥ 40,000 individual specimen records) associated with specimens in biodiversity repositories serving their data in the public domain. With our models individually M-defined to project species distributions into the biologically realistic geographical space accessible to each species (informed by PAIC-level geology, within-PAIC biogeographical information, and a synthesis of information on the evolutionary history and phylogenetic relationships of Philippine amphibians; see Brown et al. 2013 for review), we are confident of their accuracy (biological relevance) and precision (generated uniformly and, thus, comparable), at least for the for the purposes of identifying general patterns and trends in the distribution of the archipelago's amphibians.

We explored Philippine amphibian species diversity in terms of the archipelago's species richness, spatially, as modeled and quantified across cells of our presence-absence matrix, and then estimated size of the geographical distribution (average locality range size) of each species in each cell of the PAM. Relating these two indices to one other in our Range-Diversity plots, quantitatively provides a unique new perspective on several spatial biodiversity patterns that remain prevalent topics in the literature relating to the country's terrestrial biodiversity.

For example, biogeographers have long known that the southern Philippines is home exceptionally high levels of herpetological diversity (Taylor 1928; Inger 1954; Leviton 1963, Brown & Alcala 1970, 1994; see Sanguila et al., in press, for review). The knowledge, emphasized in early summaries of the archipelago's biodiversity (Dickerson 1928; Inger 1954) contributed to the perspective of the Philippines as a "fringing archipelago," in which faunal elements and colonized its chains of islands in a south-to-north manner, reaching only as far as their powers of dispersal would allow (Inger 1954; Brown & Alcala 1970; Diamond & Gilpin, 1983). Under this view of the archipelago, biogeographers reasoned that the southern islands of the Philippines held such exceptional levels of diversity as a result of proximity to a large source area, namely the islands of the Sunda Shelf with the large island of Borneo as the primary source for dispersal into the Philippines in an island-hopping manner or across land bridges during glacial expansions of polar ice caps and lowering of global sea levels (Inger 1954; Heaney 1986). Bolstered by taxonomic evidence and close inferred relationships with Bornean taxa, this view prevailed (Taylor 1928; Inger 1954; Brown & Alcala 1970) and arguably still has merit. However, the simple fringing-archipelago model did not include consideration of the evolution of species within the confines of the archipelago (*in situ* speciation) nor did it account for non-linear, two-way (e.g., including north-to-south) colonization, which has since been documented in some groups (Esselstyn et al. 2010; Linkem et al. 2013); the idea may have also predisposed biogeographers to view the northern Philippines as somewhat faunistically "depauperate"—an outcome that may have self-perpetuated as field biologists opted not to expend time and resources surveying the perceived low-diversity forests of the north (see discussion in Brown et al. 2013a, 2013b). As more literature (and vouchered specimen associated species occurrences) based on fieldwork in these areas become available, we have begun to recognize some hotspots of northern Philippine species diversity (Brown et al. 2000, 2013a; Diesmos et al. 2004; McLeod et al. 2011; Siler et al. 2011)—all of which have been confirmed here (FIGURE 1A).

Another prevalent biogeographical trend confirmed and informed by our analysis relates to areas of exceeding low species diversity. A number of areas associated with the lowest estimated species diversity in archipelago represent biologically significant, environmental barriers for amphibians. The north-central Cagayan Valley of Luzon, the Pampanga Plains of Luzon, the northeast coast of Luzon, and parts of the Zambales Mountains (broad blue areas in FIGure 1A) are exceedingly arid, and some have been historically been devoid of forests, with natural dry savannas (Heaney 1991). Other noticeable pockets of low species diversity may be real, but may also represent artifacts of inadequate sampling effort. Western Mindoro, Eastern Panay, northern Bohol, and northern Negros are each noticeably less diverse than the alternate side of each landmass (FIGure 1A), but no biodiversity survey work has been conducted in these areas whereas their more diverse halves have been the subject of intensive biodiversity survey work (Brown & Alaca 1961, 1964, 1986; Ferner et al. 2001; RMB, *unpublished data*). Finally, some areas of low predicted diversity like the northern and southern extremes of Palawan, and all of Cebu Island have been understudied and may be undersampled, but also are known for their arid environmental conditions combined with early and complete removal of their forests (Boulenger 1894; Inger 1954; Brown & Alcala 1986; Supsup et al., in press). It remains possible that some patterns elucidated here are artifacts of deforestation.

Consideration of the extremes of the bivariate distribution of points (our PAM's 5 km^2 cells) in our range-diversity plots bounds and defines the full range of amphibian communities we encounter in the Philippines. From areas of low to moderate species richness but exceedingly small geographical ranges of included species (portions of central Palawan, east Luzon coastal areas, the southern extreme of the Cagayan Valley of Luzon; FIGURE 2A) at one extreme, to areas of the archipelago's highest species richness of species with moderately sized ranges (primarily the montane forests of the Mindanao PAIC islands; FIGURE 2B), to the opposite extreme of sites with extremely low species diversity, and composed of species with exceedingly large ranges (northern portions of the Cagayan Valley, the Pampanga Plains, the northern and southern tips of Palawan, and coastal areas throughout the central West Visayan PAIC islands; FIGURE 2D), our RD plots confirm biologically meaningful, empirical observations from the literature and several generations of field biologists with extensive experience across the archipelago (Taylor 1928; Inger 1954; Leviton 1963; Brown & Alcala 1970; Brown et al. 2013b; RMB, *personal communications* with A. C. Alcala, A. C. Diesmos, A. Leviton, W. C.

Brown, J. W. Ferner, and C. D. Siler). At the intersection of these extremes, the much of the archipelago is composed of sites that exhibit moderate species diversity and moderate average geographical range size. These portions of the archipelago including the mountains of Luzon and its Bicol Peninsula, the island of Mindoro, West Visayan PAIC islands, and the lowlands of Mindanao (FIGURE 2C).

An interesting pattern is revealed by identifying the Luzon PAIC range-diversity plot points (PAM cells) versus the Mindanao PAIC data. These two major PAICs, and extremes of the geographical configuration of the archipelago, possess fundamentally different patterns of amphibian diversity as depicted in our RD plots (FIGURE 4). Although the Mindanao PAIC possesses the highest diversity measures recorded here while dominating the larger proportional range size realm of the RD extent of variation, Luzon uniquely is associated with lower-to-moderate species richness, but smaller proportional range size region of our RD extent of variation (but see unique "crescent" of sites representing Palawan; FIGURE 4). We predict that the additional ~30 species excluded from our study because they were represented by ≤ 5 occurrences, will occupy a unique realm of RD plot space (FIGURE 4). These are the species from moderately diverse amphibian communities, with microendemic mountaintop distributions on Luzon (Diesmos 1998; Diesmos et al. 2004; Brown et al. 2000, 2012, 2013a; McLeod et al. 2011; Siler et al. 2011).

Our interests in biodiversity patterns of amphibians in island archipelagos are not limited to questions of spatial biodiversity and quantitative metrics studied here. Rather, we emphasize that the applied conservation value (Villalobos & Arita 2010; Villalobos et al. 2013; Soberón & Ceballos 2011) of such studies can be utilized to inform conservation management, protected area establishment, and priority-setting decisions. Range-diversity plots can serve as a useful tool in a variety of ways (Villalobos et al. 2013) and here we have made initial progress in the exploration of empirical distribution patterns of Philippine amphibians. We take from this exercise several practical guidelines: (A) protected areas (FIGURE 3B) in the southern portions of archipelago (the Mindanao PAIC islands) are particularly important for maximally preserving sheer numbers of amphibian species; (B) Palawan (and most likely the volcanoes of southern Luzon), the entirety of which is a protected area on paper, but which is the focus of large scale commercial, government sanctioned mining operations, is a high-value target for preservation of sites with moderate endemic diversity, and species with small geographical ranges; (C) The Islands of the West Visayan PAIC, the Bicol Peninsula of Luzon, and Mindoro represent moderate priorities for protected area establishment in that they possess lower to moderate levels of species richness, and are home to species with moderate range sizes, Lastly, our results also indicate that most Philippine government protected areas have high to intermediate values of two biodiversity indices, reflecting their positive potential to preserve diverse endemic amphibian species assemblages. Exceptions exist, in both "over-protected" (protected areas in low-diversity central Mindoro, northern Palawan, and southwest Luzon) and "under-protected" ends of the spectrum (highly diverse areas lacking legal protection: highlands of Leyte Island, and the mountains of northeast Mindanao, northeast Luzon), but the current protected areas network of the Philippine government has great potential to maximally preserve Philippine amphibian species diversity if the enclosed forests are actually protected and laws aimed at curtailing unsustainable harvest of forest products are actually enforced.

FIGURES

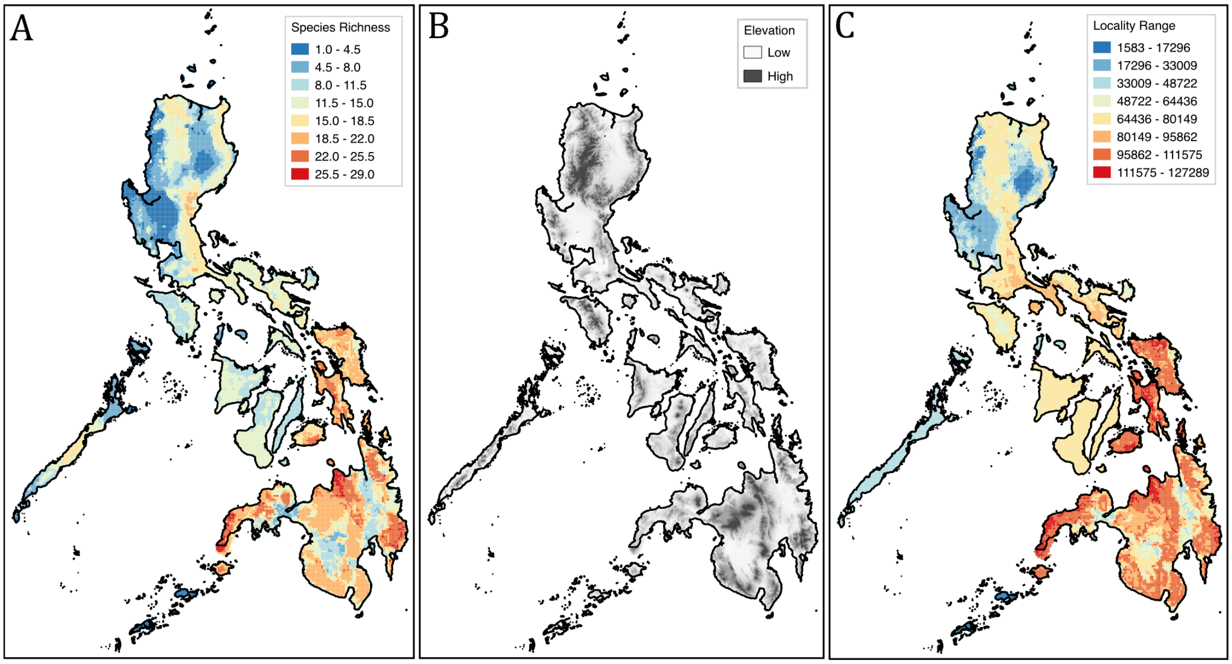

FIGURE 1. Geography of Philippine amphibian species diversity, as characterized by stacked species distribution models, compiled by a presence/absence matrix (PAM) analysis. (A) Species richness for 85% of the amphibian fauna (n=96 species for which ≥ 5 occurrences were available); warmer colors indicate higher diversity (key); (B) elevational gradients, for comparison, depicted by increasingly dark shading with high elevation; and (C) PAM-mean range size, with warner colors indicating species with larger geographical ranges (key).

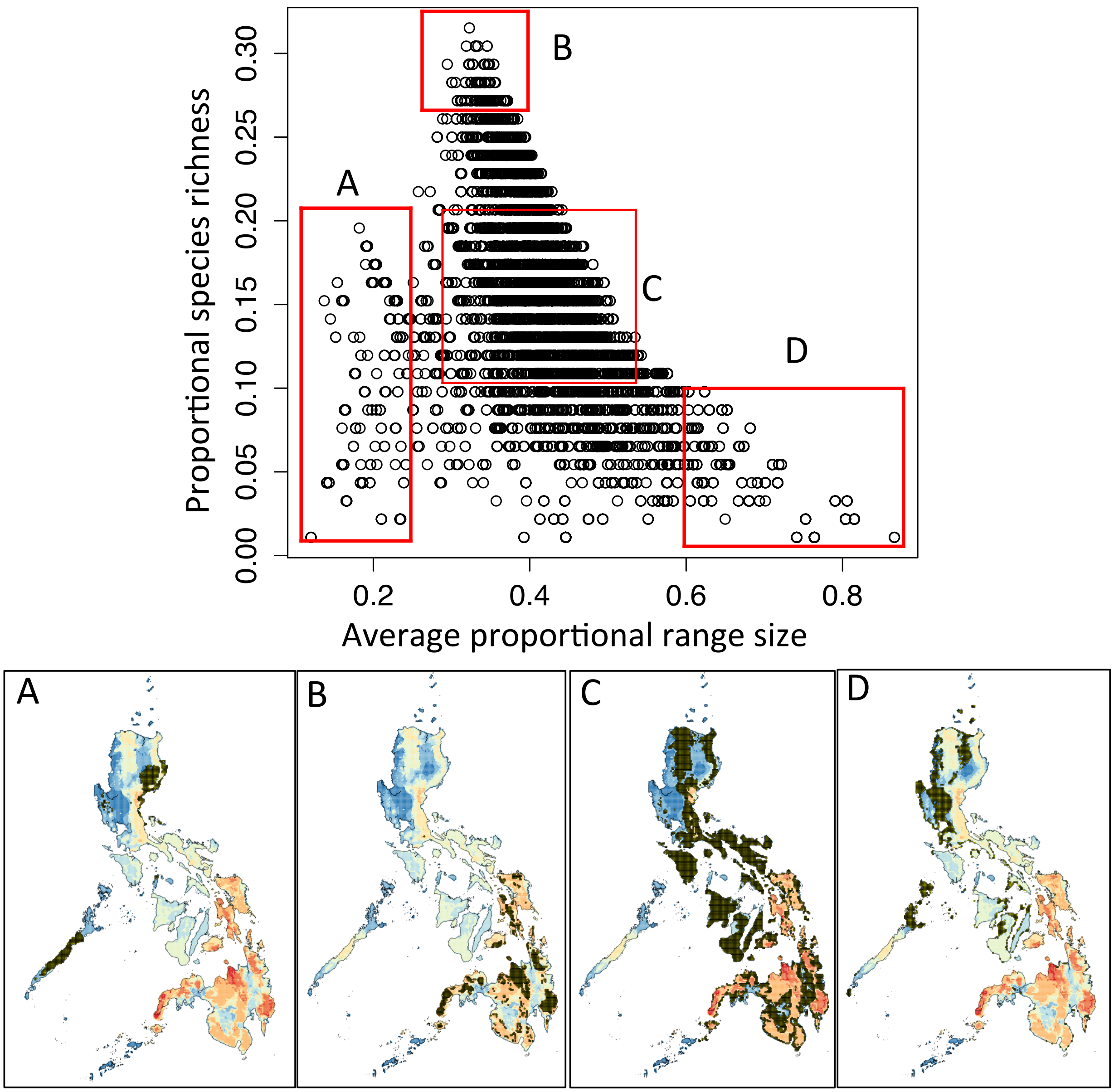

FIGURE 2. Range-diversity (RD) plot for Philippine amphibians, depicting variation in species diversity and modeled geographical range size per 5X5 km cell grid, plotted across the archipelago. Extremes of the RD plot space (boxes A–D) are highlighted (see maps) to show corresponding distribution characteristics.

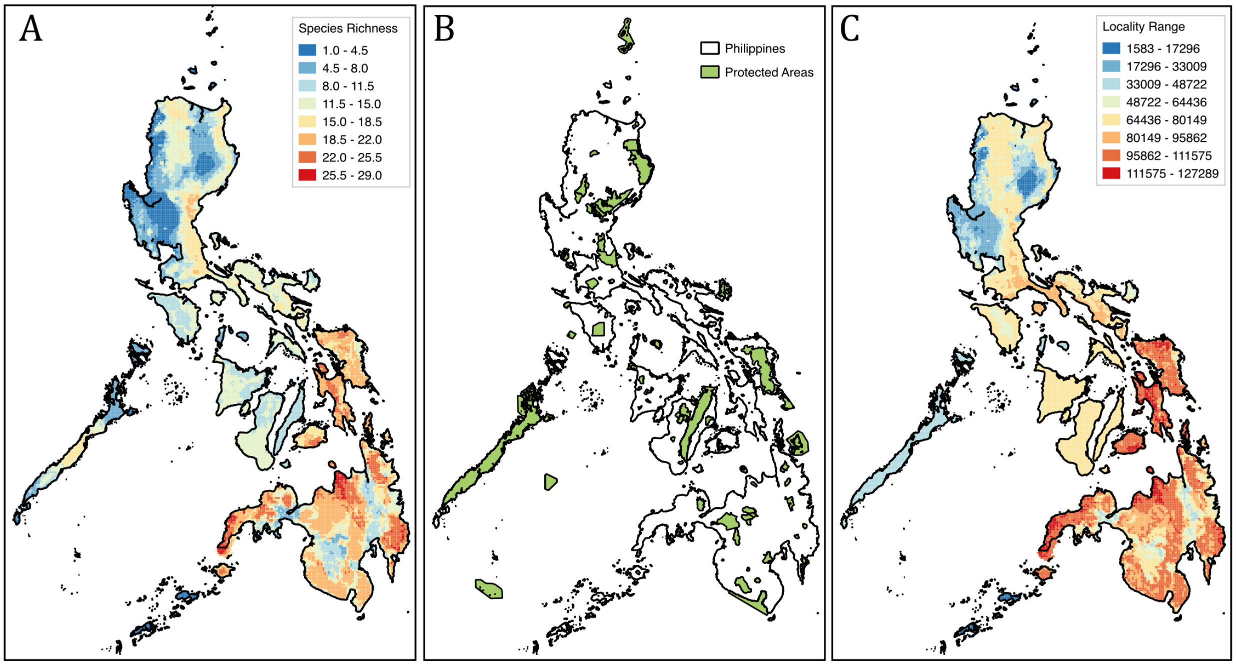

FIGURE 3. Species richness (A) juxtaposed with (B) current protected area network of the Philippines government (http://www.protectedplanet.net) and the average range size of species (C) at a given locality (PAM grid cell, 5 km^2).

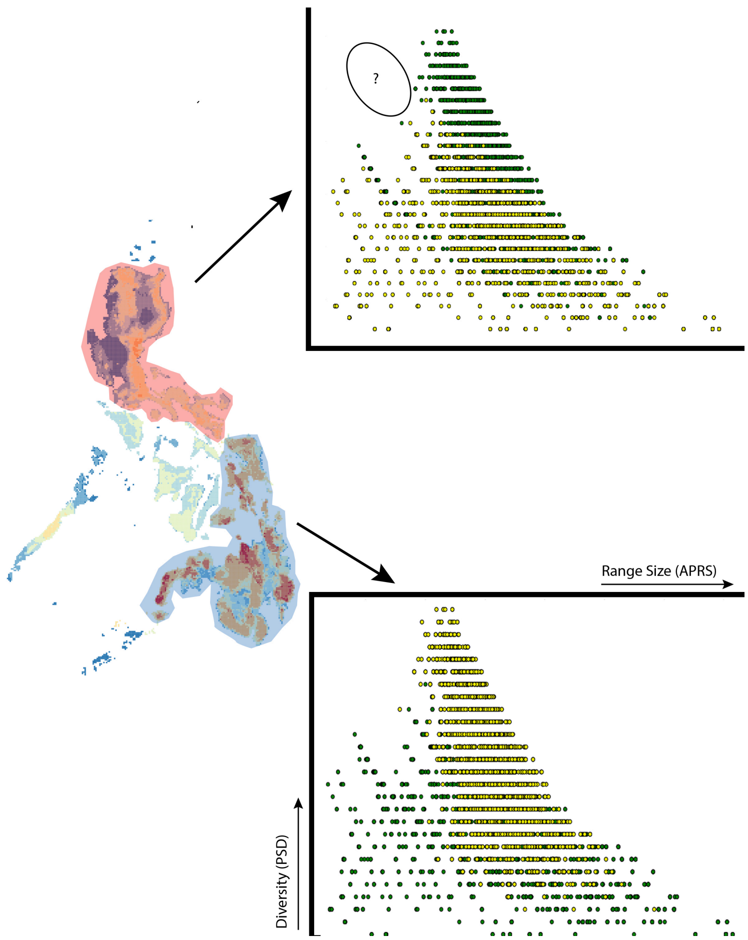

FIGURE 4. Range-Diversity plots for Luzon versus Mindanao Pleistocene Aggregate Island Complex (PAIC; Brown & Diesmos, 2002, 2009) presence-absence matrix (PAM) analysis of amphibian species diversity. In the upper panel, the ellipse enclosing a question mark ("?") indicates the approximate position of ~30 species excluded from our analysis due to insufficient numbers of unique sites records (≤ 5 occurrences); the majority of these are the microendemic mountain-top frogs of the volcanoes of Luzon, a distinct portion of the archipelago's amphibian fauna which we predict will be shown to occur in areas with moderate to high species richness, but low average proportional range sizes (see Discussion).

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